Plesiomorphic and Apomorphic Characters States in the Class Chilopoda

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ABSTRACT

The plesiomorphic and apomorphic nature of characters used for a cladistic analysis in the class Chilopoda is taken into account. The plesiomorphic or apomorphic status of the following features are proposed to be discussed here: spiracles and types of respiratory systems, coxal/anal glands (organs), spines of the first article of the female gonopod, male gonopods, testis, genital tract, supernumerary Malpighian tubules.

RÉSUMÉ

États plésiomorphique et apomorphique des caractères dans la classe Chilopoda.

La nature plésiomorphique ou apomorphique de chaque caractère utilisé pour une analyse cladistique des chilopodes est prise en compte. On propose notamment de discuter ici le statut plésiomorphique ou apomorphique des organes suivants : spiracles (stigma) et types de système respiratoire, glandes coxales/anales, gonopodes des femelles, gonopodes des mâles, testicules, tractus génital, tubes de Malpighi supplémentaires.

INTRODUCTION

In 1965 a preliminary phylogenetic tree of Chilopoda was published (PRUNESCU, 1965) already made according to cladistic principles. For the reconstruction of the morphologic characteristics of the primitive chilopods, the primitive morphologic features of representatives of the orders Scutigeromorpha and Lithobiomorpha were selected. This was followed by a synthesis of the research on the anatomy and evolution of the genital system in Chilopoda (PRUNESCU, 1969a), as well as a discussion regarding the place of some atypical chilopods regarding their systematics and evolution (PRUNESCU, 1969b). In 1985, W. DOHLE published a cladistic analysis of the main chilopod groups and suggested a phylogenetic tree resembling that published earlier (PRUNESCU, 1965). A series of morphological features are considered plesiomorphic or apomorphic by DOHLE (1985), not as a result of a critical scientific analysis, but to underline the main resemblances of chilopods ancestors with recent representatives of the subclass Notostigmophora. In in a paper describing the fossil order Devonobiomorpha, SHEAR & BONAMO (1988) dealt with cladistic analysis of several morphologic features treated by DOHLE (1985). Taking into account that some features may have been wrong appreciated by both authors, we considered necessary to reexamine them, as a contribution to the cladistic

analysis of Chilopoda. A series of features, such as male gonopods, seminal vesicles, supplementary Malpighian tubules were analysed here, for the first time.

CHILOPOD ENVIRONMENT

In our opinion, chilopods originate within the aquatic arthropods. The same opinion is shared by other authors (KRAUS & KRAUS, 1994). The primitive chilopod environment could have been wet or very wet. Most recent chilopods live within a wet environment created by forest soil, deep cracks in rock and by caves. This option satisfies the vital needs of Pleurostigmophora chilopods and offers the natural framework in which these Chilopoda evolved and diversified from the Pleurostigmophora with 15 leg-bearing segments, unequal tergal shields and anamorphic development, to elongated Pleurostigmophora with homonomous secondary segmentation and epimorphic development. We consider the above mentioned wet environment as plesiomorphic for Chilopoda.

The life environment of Notostigmophora which live and hunt in the open air, on rocky walls and open beaches is an apomorphic one, conquered by an ancestral branch of actual Notostigmophora, detached directly from the primitive Pleurostigmophora and having the rank of sister-group with the line from which the present Pleurostigmophora derived. The Notostigmophora preserved most of the plesiomorphic features of the primitive chilopods, but also adapted their metabolism and some of their organs to this different environment.

PAIRED LATERAL SPIRACLES

These structures serve a tracheal system through which gas exchange occurs at the level of the cells of the whole organism. Pleurostigmophora kept a plesiomorphic circulatory system, because their way of life did not imposed a decrease of the blood circulation.

The same type of plesiomorphic circulatory system was also maintained in Notostigmophora. Since S. HAASE (1885), the presence of mid-dorsal spiracle has been considered to have originated in displacement and subsequent median union of the two pleural spiracles. However, tracheal lungs linked by this single median spiracle are paired and are in accordance with the bilateral chilopod organization.

Radical modification of the breathing system in Notostigmophora chilopods results from the gases exchange in "tracheal lungs" between the haemolymph which contains hemocyanin and the oxygenated air, which goes through the tracheae, closed like in a glove finger. The changing of the breathing system in the ancestors of the recent Notostigmophora can be related to the life environment of these chilopods. *Scutigera* hunt almost all their life in the open air, namely in a drier environment than the humid air of leaves and humus. In our opinion, the breathing system in Notostigmophora allowed the inner humidity to be maintained through decreasing water vapour loss at the gas exchange level, in the present apomorphic environment (Fig. 1). This is why we consider that the bilateral spiracles as well as the tracheal breathing system in Pleurostigmophora has plainly plesiomorphic features. Therefore these features can be considered characteristic for the ancestor of the recent chilopods.

The presence of spiracles on leg-bearing segments with large tergites, their absence on leg-bearing segments with small tergites, and the absence of alternation which occur in the successive large tergites on segments VII and VIII, where only the leg-bearing segment VIII has spiracles, argues for the existence of these features in the ancestor of recent Pleurostigmophora. The same strict distribution of the mid-dorsal spiracles is found again in Notostigmophora: the spiracles are present on large tergites of leg-bearing segments inclusive on the unique tergite covering the leg-bearing segments VII and VIII. This homology suggests the presenceof alternation and the lack of alternation as well in the ancestor of Chilopoda (PRUNESCU, 1965).

The problem of lateral spiracles for tracheal breathing and mid-dorsal spiracles for tracheal-lungs breathing must be treated separately from the problem of spiracle distribution on leg-

bearing segments. According to the above argumentation, the tracheal breathing through pleural spiracle is a plesiomorphic feature and the tracheal-lung breathing through mid-dorsal spiracles an apomorphic one. The distribution of spiracles on leg-bearing segments with large tergites in Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha represents a plesiomorphic feature and the distribution of spiracles on every leg-bearing segments in Geophilomorpha or in the genus *Plutonium* (Scolopendromorpha) is an apomorphic one (PRUNESCU, 1965).

COXAL - ANAL ORGANS

According to ROSENBERG (1982, 1983, 1989), coxal and anal glands are respectively specialized organs for the uptake and release of water vapour and ions from and to the environment. As mentioned above, the plesiomorphic environment of chilopods was a wet one, similar to that now existing under leaves, in humus, etc. These organs are only useful in a wet environment , in order to maintain the water and ion balance of the organism. If the pheromones are eliminated together with the water vapours (LITTLEWOOD, 1983), the plesiomorphic state of these glands is not changed. The lack of these organs in most of the species of Oryidae (ATTEMS, 1929) adapted to dry environments supports the idea of the adaptational loss of these organs in such species. The life style of *Scutigera* , which hunts on stone surfaces in the open air, would not be possible, if the coxal-anal organ were maintained (Fig. 2). Therefore, we consider the coxal-anal gland as a plesiomorphic feature and its absence in Scutigeromorpha as an apomorphic feature. SHEAR & BONAMO (1988) seemed to agree this interpretation but finally consider the absence of such organs as a plesiomorphic feature and their presence as an apomorphic one.
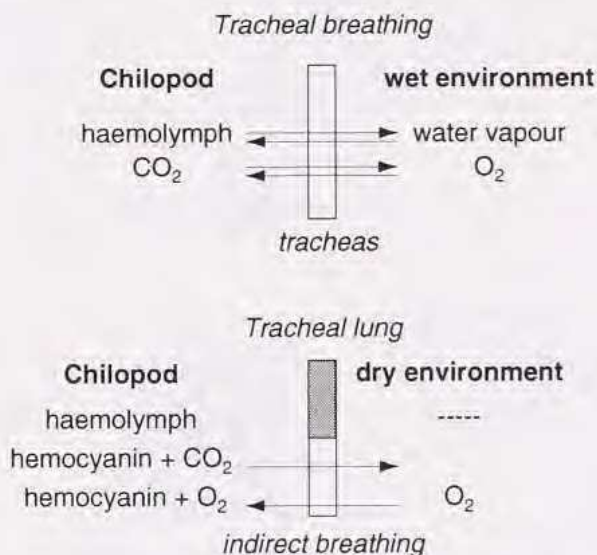

FIG. 1. — Correlation of respiration type with life environment in Chilopoda.
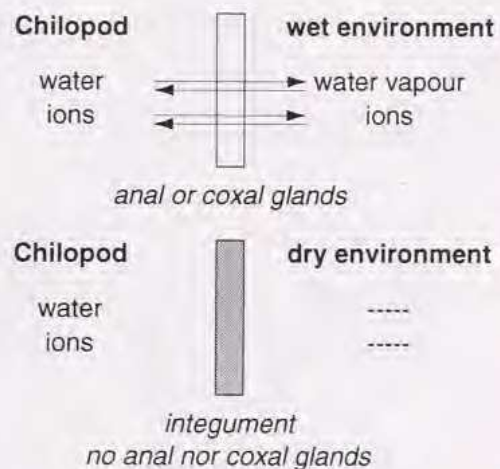
FIG. 2. — Presence and absence of coxal-anal glands in connexion with the life environment of Chilopoda.

In Lithobiomorpha, the coxal glands are located on the last 4 pairs of coxae. We consider this distribution plesiomorphic.

In Scolopendromorpha and Geophilomorpha, coxal glands are distributed on the last pair of coxae, sometimes on the margin of the respective sternite. This reduction of the coxal glands can be considered an apomorphic feature of the first degree.

The older name of "ano-genital capsule" (DOHLE, 1990) seems a misleading name for the structure of the involved organ. Its presence in Craterostigmomorpha only is apomorphic (SHEAR & BONAMO, 1988). In fact, in its two halves, this capsule contains several glands homologous to the coxal glands of other chilopods (unpubl. observations). These glands, leaving the coxae, located in an original organ. The ability of this organ to close firmly or open widely may be linked with the need to con troll water vapour exchange with the environment. A proper name would be the "capsule of coxal-anal glands". This transformation can be considered as an apomorphic feature of the second degree. The lack of coxal glands in Scutigeromorpha can be considered as an apomorphic feature of the third degree.

FEMALE GONOPODS

These organs are highly-modified ambulatory appendages (Fig. 3). As the articles of the ambulatory appendages in Scutigeromorpha and Lithobiomorpha have a large spine (macrosetae) at their distal ends, we consider that the female gonopod, which is characteristic to Lithobiomorpha and has macrosetae, is plesiomorphic.
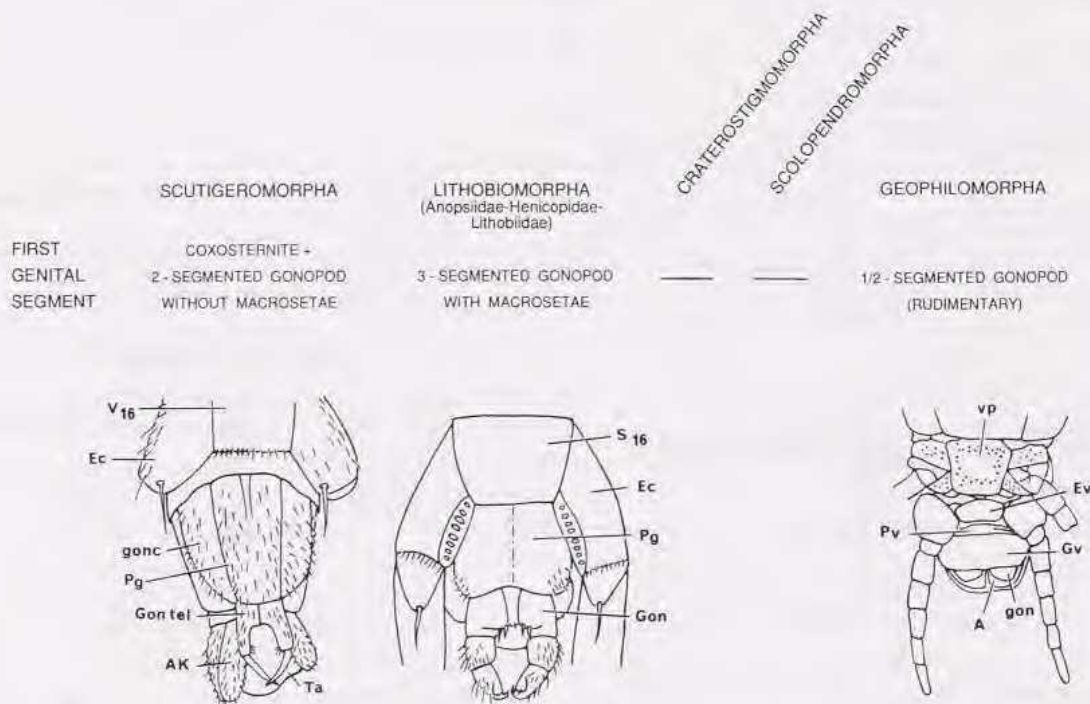

FIG. 3. — Female gonopods. (Drawings reproduced from ATTEMS, 1926). A: anal segment; AK: anal valves; Ec: coxite of the last legs; Ev: sternite of the last leg-bearing segment; gon, Gon: gonopods; gon tel: telopodite of the gonopods; gonc: coxite of the gonopods; Gp: pleurite of the genital segment; gon tel: telopodite of the gonopods; Gv: sternite of the genital segment; Pg, Pv: sternite of the pregenital segment; S_{16}: sternite of the 16th segment; Ta: tergite of the anal segment; V_{16}: sternite of the 16th leg-bearing segment; vp: sternite of the penultimate leg-bearing segment.

The two female gonopods of Lithobiomorpha are firmly separated from one another and formed of three distinct segments, while the female gonopods of Scutigeromorpha comprise two articles, the first one being partly joined (Fig. 3). The female gonopod is a plesiomorphic feature in Lithobiomorpha, an apomorphic one in Scutigeromorpha. Rudimentary female gonopods in Geophilomorpha show a greater degree of apomorphism, of the second degree. The lack of female gonopods in Craterostigmomorpha and Scolopendromorpha is equivalent to an apomorphic feature of the third degree.

MALE GONOPODS

Although the authors of the previous cladistic analysis did not deal with this feature, we think that a review of it is of phylogenetic interest.The most complete male gonopod exists in the representatives of the Henicopidae (Lithobiomorpha). Within this group, the male gonopod consists of 4 distinct segments. In comparison, the male gonopods of Lithobiidae are rudimentary. The male gonopods of Geophilomorpha are formed of two well articulated segments. The male gonopods in Scutigeromorpha are rudimentary but in two pairs (Fig. 4).
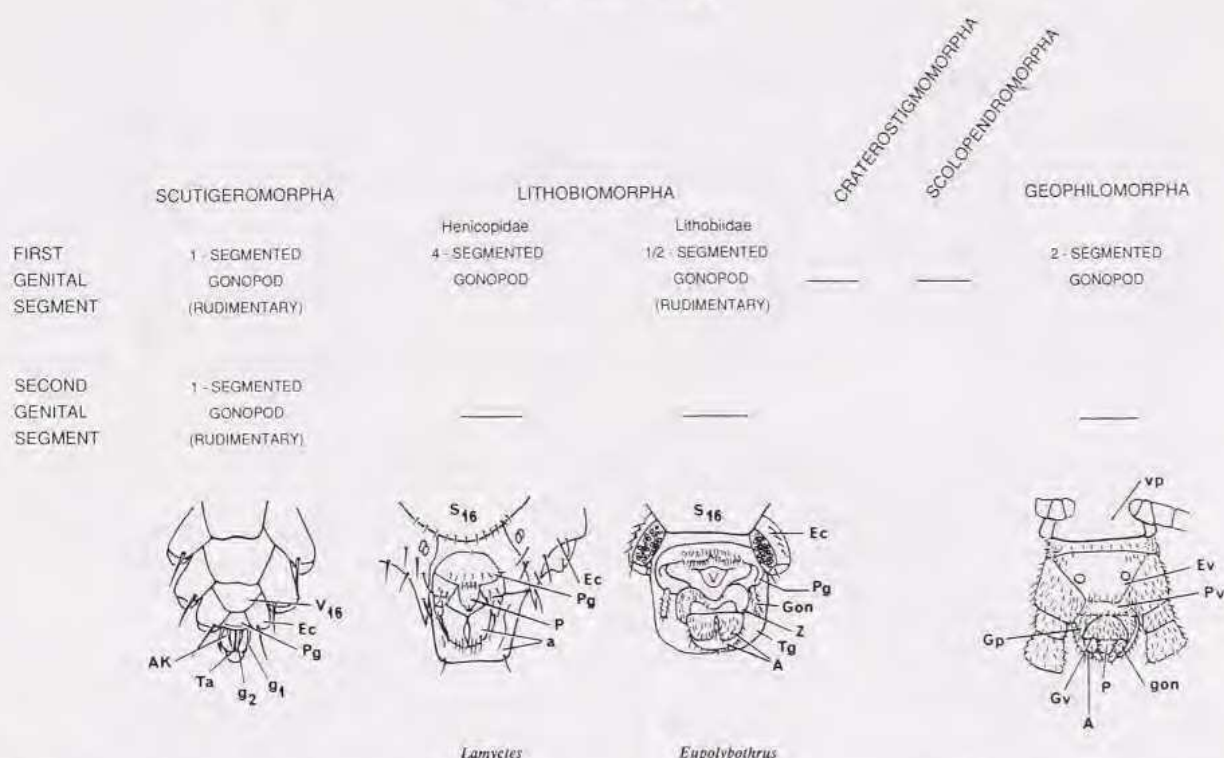
MALE GONOPOD

FIG. 4. — Male gonopods. (Drawings reproduced from ATTEMS, 1926). A, a: anal segment; AK: anal valves; Ec: coxite of the last legs; Ev; sternite of the last leg-bearing segment; g_1:pregenital segment of the gonopodes; g_2: rudimentary gonopods of the genital segment; gon, Gon: gonopods; Gp: pleurite of the genital segment; Gv: sternite of the genital segment; p: penis; Pg, Pv: sternite of the pregenital segment; S_{16} : sternite of the 16th segment; Ta: tergite of the anal segment; Tg: tergite of the genital region; V_{16}: sternite of the 16th leg-bearing segment; vp: sternite of the penultimate leg-bearing segment; Z: sternite of the genital segment.

Taking into account their number, they represent a clear plesiomorphic feature of Scutigeromorpha and are apomorphic for all the other chilopods. By the reduction in size and

number of articles, these gonopods are apomorphic. We therefore suggest the separation of "gonopod pairs number" feature from the "gonopod articles number" feature. Thus, any future cladistic analysis will be able to use both features.

The quantification of the "male gonopod articles number" feature could be made as follows:

- Henicopidae: 4 segments = plesiomorphic feature.
- Lithobiidae: rudimentary gonopods = apomorphic feature of the second degree.
- Scutigeromorpha: rudimentary gonopods = apomorpic feature of the second degree.
- Geophilomorpha: biarticulated gonopods = apomorphic feature of the first degree.
- Craterostigmomorpha and Scolopendromorpha: gonopods absent = apomorphic feature of the third degree.

TESTES AND TESTICULAR SYSTEM

In Scutigeromorpha, the male genital system consists of two testes, each formed of a macrotestis and a microtestis (PRUNESCU, 1969c). This structure can also be observed during the larval development (PRUNESCU, 1992b) and is clearly plesiomorphic (Fig. 5).
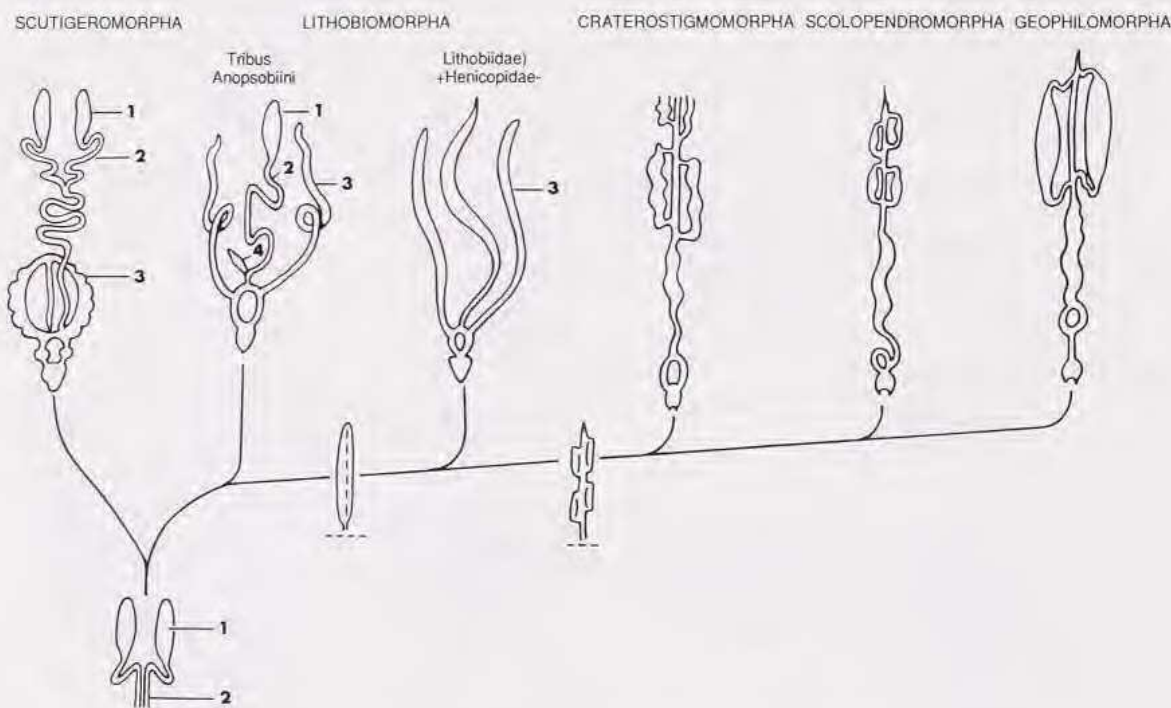

FIG. 5. — Ontogeny and phylogeny of the male genital system in Chilopoda. 1: macrotestis; 2: microtestis; 3: seminal vesicles; 4: undifferenciated rudimentary testis.

In adults of the tribe Anopsobiini (Lithobiomorpha), one testis is undifferentiated and exclusively populated with spermatogonia. The other functional one, consists of macrotestis and microtestis, as in Scutigeromorpha (PRUNESCU & JOHNS, 1969; PRUNESCU, 1992a). This testicular system is apomorphic in the first degree. *Esastigmatobius*, of the Henicopidae (PRUNESCU, MESIBOV & SHINOHARA, this volume) and numerous genera of Lithobiidae (PRUNESCU, 1964) have the testicular system formed of a single testis.

In *Lithobius forficatus*, during larval development, the unique testis results from the joining of two male gonads (BIEGEL, 1922; ZERBIB, 1966). Hence, the single testis in Lithobiidae and perhaps in Henicopidae s. str., is an apomorphic feature of the second degree.

During the larval development of Scolopendromorpha, the two embryonic testis merge to form an unpaired median organ which, by subsequent lateral burgeonings, forms a large deferens duct, to which are linked numerous, pseudometameric, testicular vesicles (HEYMONS, 1901). This is an apomorphic testicular system of the third degree.

Incomplete data for microscopic anatomy show that *Craterostigmus tasmanianus* testicular system structure is similar to that of Scolopendromorpha (PRUNESCU, MESIBOV & SHINOHARA, this volume).

The anatomic data of the testicular system in Geophilomorpha show the presence of two lateral testicular vesicles, linked by a central deferents duct. Thus, Craterostigmomorpha, Scolopendromorpha and Geophilomorpha have an apomorphic testicular system of the third degree. According to the present state of knowledge, we cannot differentiate a distinct apomorphic degree between the testicular system in Geophilomorpha with that of Scolopendromorpha.

MALE GENITAL TRACT

The male genital tract is constituted by the genital organs between the testes and the genital atrium. This anatomical structure follows a clear evolution simplification.

In Scutigeromorpha several organs play an important role in the deposition, maturation and preservation of spermatozoa. We consider that this is a plesiomorphic feature. Of this very complex and histologically varied anatomic system, only two elongated tubes are retained in Lithobiomorpha. They are named seminal vesicles and have the same role as the similar organs of Scutigeromorpha. This is an apomorphic situation of the first degree.

In Craterostigmomorpha, Scolopendromorpha and Geophilomorpha orders, the seminal vesicles are absent, their function being taken over by the posterior half of the very expended deferens duct. In this duct, the spermatozoa are deposited and the spermatophores formed (JANGI, 1956). This can be considered as an apomorphic feature of the second degree.

SUPERNUMERARY MALPIGHIAN TUBULES

Only two Malpighian tubules were known to be present in all chilopod groups (LEWIS, 1981).

In *Scutigera coleoptrata* we found a supplementary pair of Malpighian tubules, which have dorso-ventral insertion, at the level of the junction of the mid-gut with the hind-gut.

In *Craterostigmus tasmanianus* we found only one supplementary Malpighian tubule, which has a medio-dorsal insertion at the same area of the intestine, and which is directed towards the posterior region of the body (see PRUNESCU & PRUNESCU, this volume).

The presence of two supplementary Malpighian tubules in *Scutigera coleoptrata* suggests they are plesiomorphic. As a rule, in Chilopoda, the evolution presents a tendancy to simplify the features of different systems or organs. So, the absence of supernumerary Malpighian tubules in Lithobiomorpha is an apomorphic feature of the second degree. The disappearance of the ventral supernumerary tubule in *Craterostigmus tasmanianus* represents an apomorphic feature of the third degree, while the presence of the dorsal supernumerary tubule represents a plesiomorphic one. The absence of any supernumerary Malpighian tubule in Scolopendromorpha and Geophilomorpha represents an apomorphic feature of the second degree, distinct from the apomorphic feature of the second degree in Lithobiomorpha, which was realized by its own evolutive line.

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